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TRANSPOSITION, NOVELTY, AND LIMBIC LESIONS[1]

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Monkeys with amygdaloid and hippocampal lesions and an operated control group were found to have high savings upon retraining to transposed stimuli after learning of a size discrimination. None of the group differences on the savings measure approached significance. Both amygdala and control groups, however, exhibited a disruption in performance on the first 20 retraining trials, which was highly related to performance on a former novelty test. It was suggested that former reports of a transposition deficit after amygdalectomy may have been due to differences in responses to novel cue used in test pairs, and to relatively few test trials being given.

In the model of limbic system function recently presented by Douglas and Pribram (1966), the amygdala is postulated to be a vital anatomical substrate of an attention-directing system in which the probability of attention to a stimulus is increased as a function of reinforcement. This system is basically reward-sensitive, error-insensitive, and its disruption through removal of the amygdala is postulated to result in an *S* whose behavior is now largely determined by a remaining system (associated with the hippocampus) which is error-sensitive, reward-insensitive. While this hypothesis, with some elaboration, can account for the greater part of the results in the literature on the effects of amygdalectomy on behavior, there is one finding which appears to lie completely outside this line of reasoning. This glaring exception is the report that amygdalectomized monkeys do not transfer training from one discrimination problem to another when the two stimuli in each case differ in the same way along a single dimension (Bagshaw & Pribram, 1965; Schwartzbaum & Pribram, 1960). The amygdalectomized *Ss* showed no tendency to press either of the test stimuli, while the normal *Ss* responded almost exclusively to the test stimulus which had the same relative brightness or size as the one originally rewarded, even though this particular stimulus was of a different absolute size or brightness from the originally rewarded stimulus. These data imply that the amygdala is involved in an underlying mechanism which results in a transfer of training on the basis of relative differences between cues, and there is reason to believe that such a conclusion has been drawn by many workers in this field. The present author attempted to replicate the results above, as the data in these studies do not lead unequivocally to the conclusions which have been drawn. For example, the Bagshaw and Pribram (1965) study was actually an investigation of postoperative retention of a transposition tendency when the original problem had been learned preoperatively, and the results do not necessarily apply to *Ss* originally trained while lacking the amygdala. In both studies relatively few test trials were used, and since one or both of the test stimuli were novel, group differences may well have been due to differential novelty responses rather than to differences in transposition. The latter point is especially relevant, because it has been shown by Douglas and Pribram (1966) that normal and amygdalectomized monkeys differ in their responses to novel stimuli. In addition, one of the authors above had always suspected that his transposition results were somehow related to differences in general reactions to the suddenly introduced test stimuli.[2] Finally, in the second experiment reported in

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[2] K. Pribram, personal communication, 1966.

Schwartzbaum and Pribram (1960), the results were diametrically opposed to those of the first experiment, upon which most of the conclusions were based. In that second experiment *Ss* were trained to always respond to a stimulus of medium brightness, whether it was paired with a lighter or darker stimulus. Since a transposition tendency would interfere with acquisition on this task, normal *Ss* should have performed poorly in comparison to the amygdala group. In fact, however, exactly the opposite results were found, with the normal group learning in about a fifth as many trials as the amygdala group, and making only about a fourth as many "errors" (transposition responses). Since this test differed from the others in that it was much longer and presumably less sensitive to initial novelty reactions, and since in this test no deficit was found after amygdalectomy, the measure of transposition chosen for the present study involved training to respond differentially to one of a pair of stimuli which differed in size, and then retraining to another pair which differed along the same dimension. Unlike the Schwartzbaum and Pribram experiment, however, a transposition response on the retraining trials was "correct." Transposition tendencies should then show up as a positive transfer of training.

Although it was hoped that no transposition deficit would be found in amygdalectomized monkeys, in the event that such a deficit should be found it would be important to show that it was specifically related to amygdaloid removal, and not to either brain damage or limbic system lesions in general. For this reason a group of hippocampally lesioned *Ss* was tested in addition to the amygdalectomized and operated control groups.

Method

Subjects

The *Ss* were 14 immature rhesus monkeys. Bilateral hippocampectomies were performed on 4 *Ss* by aspiration through a slit in the entorhinal area. Amygdalas were removed bilaterally from 6 *Ss* by suction through the medial temporal pole. Operating procedures used on the 4 operated control *Ss* were identical to those used for the amygdalectomized monkeys except that no further damage was done after removal of part of the skull. These animals had been used in a previous series of experiments (Douglas & Pribram, 1966), and are presently scheduled for further tests. For this reason histological results will not be known for some time. The operations were performed under visual guidance, however, and identical operations by the same surgeon (Karl H. Pribram) in the past have been found to result in extensive or complete removal of the target areas, with minimal damage to surrounding tissue. Testing was not begun until several months had elapsed since surgery, and all *Ss* appeared to be fully recovered and in good health. All were on a deprivation diet consisting of about two-thirds of their usual food ration (monkey pellets), with all feeding done after completion of testing for the day.

Apparatus

Behavioral testing was done in the automated apparatus for discrete trial analysis, which is described in Pribram, Gardner, Pressman, and Bagshaw (1963). The *S* was placed in an enclosed compartment in which it sat before a 4 × 4 array of 16 depressable buttons, with a food cup located just below the buttons. Various stimuli were projected onto these clear plastic buttons from the rear. In the present case, stimuli were presented in pairs at adjacent locations, with relative positions randomly varied, but with both always appearing somewhere in the middle two rows (8 buttons). The *Ss* were watched through a one-way glass, but responses were automatically recorded on punched tape.

Procedure

The *Ss* were first trained to press the larger (or smaller) of a pair of yellow circles which were presented simultaneously. Reward was one peanut, intertrial interval was 8 sec., and the learning criterion was 36 correct on four consecutive 10-trial blocks (90%). Training was continued on the first session until either criterion had been achieved or until 100 trials had been run with little sign of progress. Actually, all but 2 *Ss* (both in the amygdala group) reached criterion levels in the first session. On the day following attainment of criterion, *Ss* were retrained to the same criterion to a new stimulus pair which consisted of one of the original circles and a new yellow circle of a size different from either of those used in the original training. Three different circles, 1, ¾, and ⅜ in. in diameter, were used in four different combinations, as shown in Table 1.

In the operated control and hippocampally ablated groups 1 *S* was randomly assigned to each sequence, as were 4 randomly chosen *Ss* in the amygdalectomized group. The remaining 2 *Ss* in the latter group were assigned to Sequences 1 and 3. It can be seen that the learning of a relative discrimination should lead to a positive transfer

TABLE 1
DIAMETERS (IN INCHES) OF CIRCLES USED IN VARIOUS TRAINING SEQUENCES

Sequence	Original training		Transposition training	
	Positive S	Negative S	Positive S	Negative S
1	⅜	¾	¾	1
2	¾	⅜	1	¾
3	1	¾	¾	⅜
4	¾	1	⅜	¾

of training, as the larger (or smaller) circle of the two was correct in both cases. The learning to press (or not press) a circle of a given diameter should, however, detract from performance on the retraining or transposition task.

Unfortunately, some *S*s learned the original problem so fast that there was little or no room for improvement on the retraining, and savings scores were rendered meaningless for these *S*s. For this reason an additional test was given which consisted of reversal training to the original stimulus pair followed by retraining to the reverse of the original transposition stimuli. In other words, the positive or negative value of the stimuli shown above was reversed, but procedures otherwise were identical to those used on the first test. As reversal generally required many more trials than original learning, it was possible to detect savings on this second test by those *S*s in which this was impossible after original learning.

Overall transposition was measured in terms of percentage of reduction in trials to criterion on the retraining tasks as compared to the maximum possible reduction. For example, if *S* required 40 trials to learn the original problem and 20 to learn the transposed problem, then this represents an improvement of 20 trials out of a maximum of 40, or 50% improvement. This method was used because it did not tend to penalize fast original learning.

RESULTS

Since transposition scores after original learning and after reversal training were almost identical for all *S*s combined (63.6% vs. 64.1% improvement, respectively), each *S* was given a composite score in order to eliminate some of the variability due to very fast original learning in some *S*s. Transposition scores, in terms of percentage of improvement on the retraining tasks, were: hippocampectomized group, 79.2%; operated control group, 63.5%; amygdalectomized group, 55.4%. None of the group differences approached statistical significance, the largest t being that between the hippocampus group and the other two combined ($t = 1.58$). Savings or improvement scores were in all cases significantly larger than a chance level of no improvement (hippocampus group, $t = 8.1$; control group, $t = 8.6$; amygdala group, $t = 5.5$; $p < .005$ in all cases). The hippocampal group averaged 20 trials to criterion in the original problem and 0 on the transposition, 145 trials to reversal and 32.5 trials to transposition of the reversal. With the control group these figures were 15 vs. 10 and 58 vs. 20; and in the amygdala group the figures for trials to criterion were 68.3 vs. 26.7, and 160 vs. 75 trials. It is doubtful that more than a small part of this marked improvement in all groups on the retraining trials, including the amygdala group, could be due to a general learning set, as these were highly sophisticated *S*s and the tasks extremely simple. Thus, when this method of measuring transposition is used, amygdalectomy appears to have produced no detectable deficit in transposition. In addition, hippocampectomy is now known to produce no deficits in transposition tendencies.

DISCUSSION

While the measure of the amount of improvement in trials to criterion indicated that all three groups had high transposition tendencies, a different conclusion would have been drawn if only the first 20 or fewer trials had been considered. On the first 20 retraining or transposition trials, both the amygdala and control groups made only a few more correct responses than they had on the original training or reversal. In terms of percentage of improvement in performance, the figures were: amygdala group, 28%; control group, 11%. The improvement in performance in these two groups combined was significantly less than that found in the hippocampal group, which averaged 60.1% ($t = 2.7$, $p < .02$). This, coupled with the fact that both groups "recovered" quickly enough to show high overall savings, indicates that performance in the amygdala and control groups may have been temporarily disrupted by some factor which rapidly dissipated. An obvious possibility is that novelty responses were de-

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tracting from performance on the early trials during retraining. This possibility was investigated by comparing present performance on these trials with the results of a novelty test which had previously been given to these same animals (Douglas & Pribram, 1966). On that test *S*s had been trained to press the most rewarded of two partially reinforced stimuli, and then these two stimuli were separately paired with a series of novel stimuli. A high negative correlation was found between *S*'s former tendency to respond to the novel stimulus in comparison to the least rewarded cue and the present degree of improvement on the first 20 retraining trials ($r = -.74$, $p < .01$). That is, the more often *S* had responded to the novel cue, the more likely it was that it would do poorly on the early transposition trials. An equally high correlation was found in the amygdala and control groups between a former indifference in choice between the novel and most rewarded cues and present success on the early trials ($r = .76$, $p < .02$). Since both the novelty and the transposition tests involved novel stimuli, and since only one test could be considered to measure transposition (the novelty test used pattern stimuli which differed on no known dimension), it is highly probable that this common variance can be attributed to the presence of a novel stimulus.

This analysis does not, however, reconcile differences between the present results and those of the first experiment of Schwartzbaum and Pribram (1960). In their study the positive stimulus of the first pair was always retained in the test pair, and only 12 test trials were given. Under these conditions the present amygdala group performed almost identically to their amygdala group (5.0 vs. 5.8 transposition responses), but the present control group differed from theirs (4.7 vs. 11 transposition responses). Their results are, however, consistent with a hypothesis that both groups had high transposition tendencies but that the normal *S*s were responding to the novel stimulus in the test pair, while the amygdalectomized *S*s either were avoiding it or were attracted to the more familiar cue. In any event, the present results indicate that the use of only a few test trials as a measure of transposition can result in performance highly determined by a response to novelty. The present results show that neither amygdalectomy nor hippocampectomy appears to reduce a tendency to learn relative differences between stimuli and to transfer this learning to a new situation. Thus, there is presently no need for any theory of limbic system function to encompass a transposition deficit after removal of the amygdala.

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